Polygyrid Land Snails, Vespericola (Gastropoda: Pulmonata), 2. Taxonomic Status of Vespericola megasoma (Pilsbry) and V. karokorum Talmadge

by

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Abstract. A type locality is designated for Vespericola megasoma (Pilsbry, 1928) and the species redescribed. Vespericola megasoma has a diagnostic spoon-shaped verge at the apex of the penis. Vespericola eritrichius (Berry, 1939), formerly synonymized with V. megasoma, is shown to be a valid species. The anatomy of Vespericola karokorum Talmadge, 1962, is described. Vespericola karokorum is localized in a few stream drainages in the Klamath Mountains. It has a diagnostic acicular verge nearly as long as the penis. Populations of Vespericola from several stream drainages adjacent to the range of V. karokorum, formerly referred to V. megasoma, are described as a new species, Vespericola klamathicus.

INTRODUCTION

This is the second (with Roth & Miller, 1993) in a series of studies on the systematics of the West American polygyrid land snail genus *Vespericola* Pilsbry, 1939. The greatest species diversity occurs in northwestern California and southwestern Oregon, where seven nominal taxa have been recognized.

Dissections of the reproductive system, which in Vespericola is often more strikingly differentiated than the shell, show that the concept of Vespericola megasoma (Pilsbry, 1928) employed in the last monograph of the genus (Pilsbry, 1940) included several distinct species. To clarify the definition of V. megasoma, which was described on shell characters alone and with a generalized type locality, we designate a type locality and describe the reproductive systems of topotypic specimens. Vespericola eritrichius (Berry, 1939), which Pilsbry (1940) regarded as synonymous with V. megasoma, is here regarded as a valid species, based on reproductive system characters.

Land snail taxonomists generally have accepted Vespericola karokorum Talmadge, 1962, as a valid species, but a report to the U.S. Forest Service (Hunt & DeMartini, 1979) called into question its distinctness from V. megasoma. We describe the reproductive system of V. karokorum and compare the species to V. megasoma. A species from

drainages adjacent to the range of *V. karokorum*, incorrectly identified by Hunt & DeMartini (1979) as *V. megasoma*, is described herein as a new species, *Vespericola klamathicus*.

MATERIAL AND METHODS

The authors collected material of the taxa discussed in this paper from 1968 to 1992; additional specimens of many were located in museum collections. Shell height and diameter are vernier caliper measurements and exclude the expanded lip of mature shells. Whorls were counted by the method of Pilsbry (1939:xi, fig. B). The density of periostracal setae was estimated by counting the number of setae per square millimeter on the shoulder of the body whorl, 0.25 whorl behind the aperture of adult specimens, at 30× magnification under a dissecting microscope with an ocular reticle. Three counts were taken per specimen and the mean (to the nearest integer) recorded.

Specimens for dissection and whole mounts of genitalia were prepared by the methods described by Roth & Miller (1993).

The following abbreviations are used: ANSP, Academy of Natural Sciences of Philadelphia; BR, senior author's collection, San Francisco, California; CAS, California Academy of Sciences; FMNH, Field Museum of Natural



Figures 1-5

Vespericola megasoma (Pilsbry). Figures 1–3. Topotype, shell, BR 1743, CALIFORNIA: Humboldt County: along right bank of Prairie Creek near south end of Prairie Creek Redwoods State Park. W. B. Miller, B. Roth coll., 11 February 1991; top, side, and basal views. Diameter 12.7 mm. Figures 4, 5. Shell, BR 1728, CALIFORNIA: Marin County: Inverness. B. Roth, W. B. Miller coll., 29 April 1990; top and side views. Diameter 15.1 mm.

History, Chicago; LACM, Los Angeles County Museum of Natural History; MCZ, Museum of Comparative Zoology, Harvard University; SBMNH, Santa Barbara Museum of Natural History; SDNHM, San Diego Natural History Museum; USNM, United States National Museum of Natural History, Smithsonian Institution.

SYSTEMATICS

Polygyridae Pilsbry, 1895

Vespericola Pilsbry, 1939

Vespericola Pilsbry, 1939.xvii. Pilsbry, 1940:892-894. Zilch, 1960:586. Roth & Miller, 1993:135.

Type species: Polygyra columbiana pilosa Henderson, 1928 [= Vespericola pilosus (Henderson)], by original designation.

Vespericola megasoma (Pilsbry, 1928)

(Figures 1-8)

(?) Polygyra germana variety megasoma Dall, 1905:26 [nomen nudum].

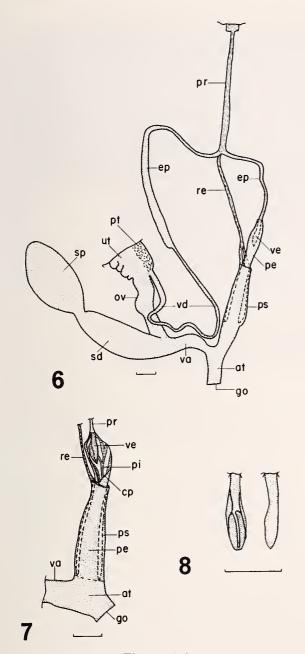
Polygyra columbiana megasoma Dall, Pilsbry, 1928:182–183, 185, figs. 8, 8a, 9.

Vespericola megasoma ('Dall,' Pilsbry), Pilsbry, 1940:894,

904-909 (in part), figs. 512B; 513:8, 8a, 9; 519. Ingram, 1946:93. Ingram & Lotz 1950:26-27, pl. 5, figs. 9, 10. Polygyra megasoma 'Dall,' Pilsbry, Baker, 1962:13.

Diagnosis: A small to medium-sized *Vespericola* with depressed-globose, almost imperforate shell of 5.5–6.0 whorls; periostracal setae 25–70/mm². Penis short, about half enclosed in sheath; with moderately long, spoon-shaped verge; spermathecal complex massive, larger than penial complex.

Description of shell: Shell depressed-globose, with 5.5-6.0 whorls. Spire moderately elevated, straight-sided or slightly convex; suture moderately impressed; whorls slightly shouldered. Periphery broadly rounded, sometimes slightly compressed toward shell axis. Embryonic whorls with smooth initial tip, thereafter rather coarsely papillose, papillae tending to fuse into collabral rugae. Post-embryonic sculpture of low, retractive growth rugae, strongest below suture. Periostracum bearing dense pile of short, closely spaced, erect, acute setae in steeply descending rows. Setae variable in density, 24–70/mm². (Paratype with 33–34 setae/mm²; holotype with glue at the usual spot where we measure setae, but right behind it, 30 ± 3 setae/mm².) Surface between setae with very fine, predominantly axial, wrinkling, sometimes elaborated into minute scales. Base



Figures 6-8

Vespericola megasoma (Pilsbry). Drawings made from projection of stained whole mounts. Scale line = 1 mm. Figure 6. Anterior portion of reproductive system of topotype, SBMNH 78000, CALIFORNIA: Humboldt County: along right bank of Prairie Creek near south end of Prairie Creek Redwoods State Park. W. B. Miller, B. Roth coll., 11 February 1991. Figure 7. Anterior portion of reproductive system of specimen SBMNH 77924, with apex of penis opened to show verge and papillose pilasters; CALIFORNIA: Humboldt County: confluence of Jordan Creek and Eel River. W. B. Miller coll., 11 April 1990. Figure 8. Ventral and lateral views of verge of specimen SBMNH 77935, ORE-GON: Curry County: Ophir, in willows behind beach. W. B. Miller coll., 24 September 1990. Abbreviations used in anatomical drawings: at, atrium; cp, cut edge of penis; ep, epiphallus;

tumid, solid-looking, radially wrinkled, densely papillose where setae worn off. Umbilicus a minute, oblique perforation. Body whorl deep, deflected downward just behind lip. Aperture broadly auriculate; plane of aperture at angle of 28° to shell axis. Lip turned outward and reflected, strongly thickened. Parietal callus extending well to left of columella in basal view. Low parietal lamella often present. Inner part of basal lip straight, narrowed. Inner lip dilated backward so as to enclose umbilicus from left side. Periostracum brown (faded to tan in holotype and paratype); lip white; yellowish-cream specimens occasionally found.

Dimensions of holotype: Diameter (exclusive of expanded lip) 12.5 mm, height 8.8 mm, whorls 5.75.

Measurements and counts of material at hand: Range of adult shell diameter 11.3–15.1 mm (mean of 45 specimens including holotype, 12.85 mm); height, 6.9–10.3 mm (\bar{x} = 8.93 mm); height/diameter ratio, 0.61–0.82 (\bar{x} = 0.694); number of whorls, 5.2–6.1 (\bar{x} = 5.61).

Description of soft anatomy: Eleven topotypes from Prairie Creek Redwoods State Park were dissected. A total of 111 specimens from various other localities was dissected.

Living animal light tan to pinkish buff along foot, darker and grayish brown on body-stalk. Mantle over the lung 10-30% maculated with black.

Atrium (Figure 6) of moderate length for the genus. Penis elongate-conical, with anterior, basal half enclosed in thin sheath adnate to base. Penial retractor muscle inserted on epiphallus. Narrow retentor muscle extending from penial retractor muscle at attachment on epiphallus to summit of penial sheath, from which other thin retentor fibers form connections with parts of epiphallus and vas deferens. Sheathed part of penis in figured topotype about 3.0 mm long; protruding part about 2.6 mm long. In remaining topotypes, sheathed part 2.4-3.3 mm (mean 2.8 mm); protruding part 2.4-3.6 mm (mean 3.0 mm). Ratio of protruding length to sheathed length 1.18-0.43 (mean about 1.0). Peduncular section of about 1.5 mm present between base of sheath and junction with atrium. Apex of penis containing moderately long, spoon-shaped verge, 1.2-1.4 mm long, 0.2 mm wide at base (Figures 7-8). Seminal duct opening into penial chamber at tip of verge through open, terminal groove with thickened edges. Inner wall of penis with papillose, anastomosing, more or less oblique pilasters.

Spermathecal duct massive, appressed to the free oviduct (which is smaller in diameter and branches from it), elongate-ovate, about 4.5 mm long, about 1.0 mm in diameter at junction with oviduct, gradually enlarging to maximum of 1.7 mm before tapering to 0.5 mm constriction at base of spermatheca. Spermatheca oblong-ovate in fully mature

go, genital orifice; ov, oviduct; pe, penis; pi, pilaster; pr, penial retractor; ps, penial sheath; pt, prostate; re, retentor; sd, spermathecal duct; sp, spermatheca; ut, uterus; va, vagina; vd, vas deferens; ve, verge.

specimens, narrowly cylindrical in less mature individuals, about 4.5 mm long, with rounded tip.

Type material: Holotype: ANSP 11140a (shell), CALIFORNIA: Humboldt County. H. Hemphill coll. Type locality here restricted to: CALIFORNIA: Humboldt County: right (east) bank of Prairie Creek, near south end of Prairie Creek Redwoods State Park.

Paratype: ANSP 11140 (shell), with same locality data as holotype.

Referred material: OREGON: Curry County: Humbug Mountain (SBMNH); Ophir (SBMNH 77935). CALI-FORNIA: Humboldt County: Prairie Creek Redwoods State Park (BR 1743, CAS 047737, SBMNH 78000); Trinidad (SBMNH); Table Bluff (BR 1744, SBMNH); ravine between E bank of Eel River and Shively Road, 10.6 km E of junction with U.S. Highway 101 (BR 1745, SBMNH); Jordan Creek at confluence with Eel River (SBMNH 77924). Mendocino County: Chadbourne Gulch (SBMNH); mouth of Tenmile River (CAS, SBMNH). Sonoma County: Green Valley (SBMNH); Hampton Road, N of Occidental (BR 1330); Wright Beach (BR 1669, SBMNH); Portuguese Beach (BR 413, SBMNH); 3.2 km N of Freestone (BR); Salmon Creek at Freestone (BR 1862). Marin County: Inverness (BR 1728, CAS 052393, SBMNH; Pilsbry, 1940).

Remarks: Following the monograph of Pilsbry (1940), the name Vespericola megasoma generally has been applied to specimens in which the inner part of the basal lip, in umbilical view, is straight or very weakly deflected forward, and the inner lip is fan-shaped and dilated such that its free edge encroaches on the umbilicus from the left side. The holotype is a shell of this type. Material with this character, however, includes several genital types that undoubtedly represent separate species, raising the question of the identity of "true" V. megasoma.

The first use of the epithet "megasoma" was Dall's (1905) Polygyra germana variety megasoma, a nomen nudum. Pilsbry (1928) validly described the species, attributing the name to Dall as a courtesy but not using Dall specimens or manuscript. No manuscript type material of Polygyra germana variety megasoma Dall is known to exist (Pilsbry, 1928: Boss, Rosewater, & Ruhoff, 1968). Pilsbry (1928) based his description on a shell received from Henry Hemphill. The original label states, in Hemphill's writing: Helix columbiana var./Humboldt Co. Cal. Pilsbry (1928, 1940) and Baker (1962) referred to the type specimen as a neotype, but because the name was validly proposed first by Pilsbry (1928), it is a holotype.

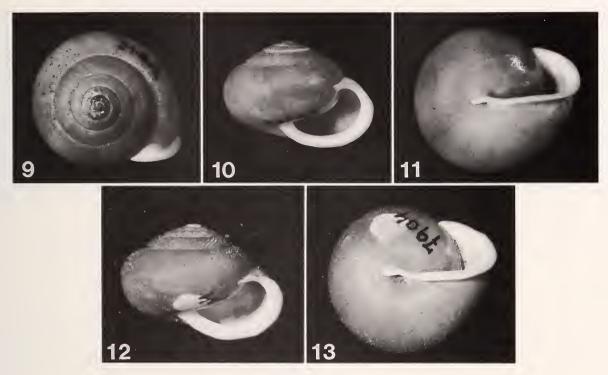
Shells with shape, dimensions, whorl count, and setation like the holotype and paratype occur in the population along the east bank of Prairie Creek, near the south end of Prairie Creek Redwoods State Park, Humboldt County, California. We designate this locality as the type locality of *Vespericola megasoma*. No other historical records exist to indicate where Hemphill might have collected the holotype; indeed, he sometimes lumped under a single locality

specimens from numerous stations (Coan & Roth, 1987). However, the designated type locality is and has long been accessible from the main north-south road (now U.S. Highway 101) through northwestern California and is at least as plausible as any other potential type locality.

The reproductive system of specimens from the type locality is as described above, with moderately large, spoonshaped verge in a rather small, slender, cylindrical penis; sheathed and protruding parts of the penis about equal in length; and a massive spermathecal complex larger than the penial complex. These characters distinguish *V. megasoma* from all other species. *Vespericola eritrichius*, which Pilsbry (1940) synonymized with *V. megasoma*, differs in having a short, conical verge in a longer penis, and a longer vagina with a fleshy thickening just below the origin of the spermathecal duct. *Vespericola klamathicus*, sp. nov., described below, has a short, conical verge with a cleft tip, and a longer penis. Several other species with distinctive genital types occur in northern California and will be described in a later paper.

Vespericola megasoma is the most widespread of the species with "V. megasoma-type" shells. Associating the name V. megasoma with the presence of a spoon-shaped verge (as we have done by designating the type locality above) preserves the accepted meaning of the name to the greatest extent possible. It means that most literature references and museum lot identifications of V. megasoma probably remain correct. However, especially with specimens from new localities, it is always desirable to establish a sample's identity by dissection.

Identifications of specimens from the localities listed above have been confirmed by dissection. In addition, we have noted shells of the V. megasoma type in museum and private collections from the following localities. Some, perhaps most, may represent V. megasoma, but pending examination of the anatomy of specimens from these localities, we regard this material as indeterminate: OREGON: Douglas County (CAS 052416; Pilsbry, 1940): Elkton (CAS 047735). Josephine County: 5.6 km SW of Wilderville (BR 389). Curry County: Pistol Creek Camp (SBMNH). CALIFORNIA: Del Norte County: near Fort Dick (CAS 052391); 5 km N of Crescent City (CAS 047743; Pilsbry, 1940); Smith River near Hiouchi Bridge (BR 579, SBMNH); 5 km below Hiouchi Bridge (SBMNH); woods near Crescent City (Pilsbry, 1940); Crescent City (CAS 047736); Enderts Beach (BR 578; CAS 047733); E side of Howland Hill (Pilsbry, 1940); Del Norte Coast Redwoods State Park (BR 577); 3.2 km N of Requa (CAS 052380); Terwah (CAS 052266; CAS 052403); across Klamath River from Requa (Pilsbry, 1940); Chaffey Ranch, 11 km above mouth of Klamath River (SBMNH). Humboldt County: 5 km N of Orick (CAS 052271); mouth of Redwood Creek (BR 1000); Orick (CAS 047740, CAS 047744, CAS 047748, CAS 049817); Moonstone Beach (BR); Clam Beach (BR 352; Pilsbry, 1940); McKinleyville (BR 351); between McKinleyville and Mad River (CAS 052414); near Eureka (CAS 046504, CAS 047730, CAS



Figures 9-13

Vespericola eritrichius (Berry). Figures 9, 11. Paratype, shell, SBMNH 34245, top and basal views. Diameter 15.7 mm. Figure 10. Holotype, shell, SBMNH 34244. Diameter 14.4 mm. Figures 12, 13. Shell, SBMNH 77904, CALIFORNIA: Humboldt County: ravine between E bank of Eel River and Shively Road 10.6 km E of U.S. Highway 101. W. B. Miller coll., 12 April 1990; side and basal views. Diameter 14.0 mm.

047731, CAS 052415, CAS 052418; Pilsbry, 1940); Grizzly Creek (SBMNH); near Ferndale (SBMNH); sea cliff S of Centerville Beach (BR 339); Capetown (BR 328, SBMNH); Little Burr Creek, 8 km SE of Bridgeville (SBMNH); Pepperwood (SBMNH); Bridge Creek (SBMNH); Dyerville (BR 273); Miranda (BR 1186); Weott (CAS 052423) and 13 km E (BR 245, SBMNH); Fort Seward (BR 278); S Fork of Eel River near Canoe Creek (SBMNH); near Richardson Grove (BR 1746). Mendocino County: Red Mountain Creek (SBMNH); DeVey Redwood Park, S Fork of Eel River (BR); 4.6 km S of Rockport (SBMNH); N Fork of Juan Creek (CAS 052283, SBMNH); 18 km N of Fort Bragg (CAS 047754, CAS 052408); Van Damme State Park (CAS 052277, CAS 052410); 1.6 km S of Little River (CAS 052412); Navarro (BR 285, CAS 052335); Irish Gulch (BR 1673, SBMNH); Anchor Bay (SBMNH); 6.4 km E of Anchor Bay (CAS 052407). Sonoma County: 7 km S of Stewarts Point (SBMNH); Rio Nido (CAS 052357, CAS 052369); Sonoma (CAS 047811); mouth of Russian River (BR 1680); Smith Creek (CAS 047792, CAS 047793); Forestville (BR 573).

Vespericola megasoma is found in a wide variety of habitats: among moist ferns, grasses, Rubus vines, moss, horsetails (Equisetum spp.), salal (Gaultheria shallon), and other

coastal brushfield vegetation; in redwood forest. At Table Bluff Light, Shively Road, and Chadbourne Gulch it is sympatric with *Vespericola eritrichius*.

Vespericola eritrichius (Berry, 1939)

(Figures 9–16)

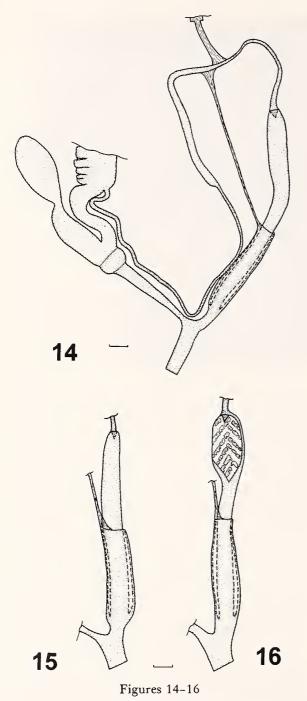
Mesodon (megasoma, subsp.?) eritrichius Berry, 1939:56, figs. 1B, 1C.

Vespericola megasoma ('Dall' Pilsbry), Pilsbry, 1940:904, 907-909 (in part), figs. 520B, 520C.

V[espericola]. eritrichius (Berry), Talmadge, 1962:29.

Diagnosis: A medium-sized *Vespericola* with depressed-globose, almost imperforate shell of 5.3-5.9 whorls; periostracal setae 12-34/mm². Penis long, slender, approximately half enclosed in sheath; with small, short, conical, pointed verge, 0.4-0.5 mm long; spermathecal duct thick, ovate or cylindrical, abruptly tapering to constriction at spermatheca.

Description of shell: Shell of medium size for the genus, compact, depressed-globose, almost imperforate, of 5.3–5.9 whorls; base inflated, solid-looking. Spire broadly conic, moderately elevated, its sides weakly convex; whorls somewhat flattened, suture shallowly impressed. Embry-



Vespericola eritrichius (Berry). Drawings made from projection of stained whole mounts. Scale line = 1 mm. Figure 14. Anterior portion of reproductive system of specimen SBMNH 77904, CALIFORNIA: Humboldt County: ravine between E bank of Eel River and Shively Road 10.6 km E of U.S. Highway 101. W. B. Miller coll., 12 April 1990. Figure 15. Penis of topotype, SBMNH 77815, CALIFORNIA: Humboldt County: base of Table Bluff. W. B. Miller coll., 9 July 1989. Figure 16. Penis of specimen SBMNH 78003, with apical portion cut open to show verge and papillose pilasters; locality same as in Figure 14 above, W. B. Miller, B. Roth coll., 11 February 1991.

onic whorls 1.4-1.6, projecting, sculptured with crowded, round or radially elongate papillae that tend to align in radiating rows separated by shallow grooves. Early neanic whorls with fine, slightly retractive growth rugae and rather sparse, erect, acicular setae in protractive, descending rows. Setae not obviously forked at base, often with small, finlike basal extension abaperturally. Periostracum between setae radially wrinkled and densely granulose with a collabral trend, some granules elaborated into minute scales. Setae closer together and shorter on subsequent whorls; 12-34 setae/mm² on shoulder of body whorl behind lip. Body whorl deep; periphery inflated, broadest just above middle of whorl. Base densely and regularly setose. Last whorl not markedly descending, sharply constricted behind lip. Aperture auriculate, peristome weakly concave in profile, oblique, at angle of about 35° to vertical; lip expanded and reflected, most strongly at base, well thickened with callus. Umbilical crevice extremely narrow, oblique. Inner part of basal lip straight or weakly kinked forward, sometimes bearing small callus nodule; inner lip dilated so that it encroaches on, and nearly covers, umbilicus from left side. Parietal callus granulose, free edge strongly convex, swinging well to left of umbilicus, with shallow sinus below upper limb of peristome. Minute, white or translucent parietal lamella usually present on inner part of parietal callus. Shell light reddish brown or yellowish brown, zone of internal callus thickening behind peristome lighter; peristome cream-colored.

Dimensions of holotype: Diameter 14.4 mm, height 10.2 mm, whorls 5.8.

Measurements and counts of material at hand: Range of adult shell diameter 11.0–14.4 mm (mean of 22 specimens including holotype, 13.09 mm); height, 8.2–10.9 mm (\bar{x} = 9.55 mm); height/diameter ratio, 0.68–0.78 (\bar{x} = 0.730); number of whorls, 5.3–5.9 (\bar{x} = 5.66).

Description of soft anatomy: Only one topotype was found; its dissection revealed a distinctive penial complex (Figure 15), but the spermathecal complex was immature. Mature specimens from another locality are illustrated in Figures 14 and 16. Ten other specimens from different localities were dissected to determine the range of variation in diagnostic structures.

Living animal tan along foot with occasional pinkish cast along edge, darker and grayer on body stalk. Mantle over lung clear buff, 20–40% maculated with black.

Atrium (Figure 14) moderate to long for the genus. Penis long, cylindrical, moderately slender, gradually tapering at apex; with anterior half enclosed in thin sheath adnate to base. Penial retractor muscle inserted on epiphallus. Thin retentor muscle extending from penial retractor at attachment on epiphallus to summit of penial sheath, from which other fibers connect with parts of epiphallus and vas deferens. Sheathed part of penis in topotype about 4.5 mm long; protruding part about 5.2 mm long. In other specimens, sheathed part 4.0–5.6 mm (mean 5.0 mm);



Figures 17-19

Vespericola karokorum Talmadge. Shell, SBMNH 78124, CALIFORNIA: Humboldt County: Wilson Creek, ca. 2.5 mi [4.0 km] NE of Orleans, upstream (west) of Ishi Pishi Road, W. B. Miller, B. Roth coll., 9 April 1992; top, side, and basal views. Diameter 15.0 mm.

protruding part 4.0-6.6 mm (mean 5.5 mm). Ratio of protruding length to sheathed length 0.87-1.47 (mean about 1.1). Slender peduncular section of about 1.0 mm present between base of sheath and junction with atrium. Apex of penis containing short, conical, pointed verge, 0.4-0.5 mm long, 0.4 mm wide at base. Seminal duct opening into penial chamber at tip of verge. Inner wall of penis with discontinuous, diverging, papillose pilasters (Figure 16).

Spermathecal duct in fully mature specimens massive, tightly appressed to free oviduct (which is smaller in diameter and branches from it), ovate or cylindrical, about 4.0 mm long, about 1.5 mm in diameter at junction with oviduct, tapering somewhat abruptly to 0.5 mm constriction at base of spermatheca. Spermatheca oblong-ovate in fully mature specimens and narrowly cylindrical in less mature individuals, averaging about 3.8 mm in length, with rounded tip.

Vagina notably long and slender for the genus. Fleshy thickening present around vagina just below junction of oviduct and spermathecal duct in fully mature specimens, partially formed or absent in immature specimens.

Type material: *Holotype*: SBMNH 34244 (shell). CAL-IFORNIA: Humboldt County: foot of bluff on ocean side of peninsula at Table Bluff Light; among moist ferns, poison oak, wild blackberries, *Equisetum*, etc. L. Shapovalov, E. H. Vestal coll.

Paratypes: CAS 064419 (shell), CAS 065908 (shell), SBMNH 34245 (11 shells), from same locality as holotype.

Referred material: CALIFORNIA: Humboldt County: base of Table Bluff, SW end of Humboldt Bay (BR, SBMNH 77815); S bank of Eel River at highway bridge at Fernbridge (SBMNH); ravine between E bank of Eel River and Shively Road, 10.6 km E of junction with U.S. Highway 101 (BR, SBMNH 77904, SBMNH 78003). Mendocino County: Chadbourne Gulch (SBMNH); Frank and Bess Smithe Redwoods State Park (SBMNH).

Remarks: Two species of *Vespericola* occur sympatrically at Table Bluff, the type locality of *V. eritrichius: Vespericola megasoma* with its diagnostic spoon-shaped verge, and a second species in which the penis is longer and the verge is small and conical, with the seminal duct opening at the tip. Our dissected topotype (Figure 15) had 22 setae/mm² on the body whorl and penultimate whorl; confirmed *V. megasoma* from the same locality had 25, 36, and 40 setae/mm². Among all dissected specimens with small conical verge and anatomy as described above, setae ranged from 12 to 34 ($\bar{\mathbf{x}} = 20.1$; n = 12).

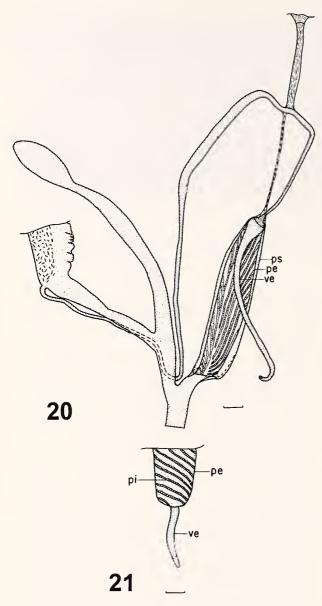
Vespericola eritrichius was described solely from shells. The holotype has 19 setae/mm². We cannot rule out the possibility that it may have had a spoon-shaped verge, but on the basis of the relatively low count of setae, we interpret it as belonging to the species with a small conical verge. The paratypes have 28–34 setae/mm²; some or all are probably V. megasoma. (There is a double irony in the fact that, although Berry emphasized dense setation in the description and name of V. eritrichius, the holotype is the specimen from the type lot with the sparsest setae—and also the one that is most probably not V. megasoma.)

Vespericola eritrichius is distinguished anatomically from other species by its very short conical verge in a long, narrow, cylindrical penis, of which the protruding portion is about equal to or longer than the sheathed portion, in combination with a massive spermathecal duct and a fleshy ring at the apical end of a long, slender vagina. There appear to be no shell characters that will always separate V. eritrichius from V. megasoma.

Talmadge (1962) treated *V. eritrichius* as a distinct species but did not discuss his reasons for doing so.

Vespericola eritrichius is found along streams, in willows and ferns; in coastal brush; and under logs and in leaf litter in mixed evergreen forest.

For purposes of the American Fisheries Society list of the common names of mollusks (Turgeon et al., 1988) and



Figures 20-21

Vespericola karokorum (Talmadge). Drawings made from projections of stained whole mounts. Scale line = 1 mm. Figure 20. Anterior part of reproductive system of topotype, SBMNH 78119, CALIFORNIA: Humboldt County: Sawmill Gulch between Ishi Pishi Road and Klamath River, W. B. Miller, B. Roth coll., 8 April 1992; penis cut open to show pilasters and verge. Figure 21. Everted penis and protruding verge, topotype, BR 1438, CALIFORNIA: Humboldt County: Sawmill Gulch between Ishi Pishi Road and Klamath River, B. Roth coll., May 1981.

other administrative uses, we proposed the name "velvet hesperian."

Vespericola karokorum Talmadge, 1962

(Figures 17-21)

Vespericola karokorum Talmadge, 1962:28-29, pl. 5, figs. 1-3. Sphon, 1971:26.

Diagnosis: A medium-sized to large *Vespericola* with depressed-conic, almost imperforate shell of 5.5-6.2 whorls; periostracal setae approximately 2/mm². Penis approximately 70% enclosed by sheath; with 10 mm long, acicular verge which extends below sheathed part of penis into peduncular section.

Description of shell: Shell medium-sized to large for the genus, depressed-conic, of 5.5-6.2 whorls; base compressed; umbilicus minute, usually not visible in direct basal view. Spire low, very broadly conic, its sides straight or weakly convex; whorls well rounded, suture moderately to strongly impressed. Embryonic whorls 1.5, first 0.25 whorl smooth, thereafter sculptured with riblets radiating from suture, almost entirely broken into rows of radially elongate papillae that tend to fade out at or just above periphery. Early neanic whorls with fine growth rugae and sparse, translucent, erect, gently curving, acicular setae in very shallowly descending rows (also aligning in nearly collabral series). Setae minute at first but rapidly increasing in size, to 0.4 mm long on third whorl, 1.0 mm on fourth whorl; longest setae, on periphery of body whorl, 1.1-1.3 mm long; spacing of setae generally about 2/mm². Zone of small (0.2 mm or less) setae usually present just below suture. Periostracum between setae densely granulose. Periphery rounded to subangulate, broadest above middle of whorl, somewhat sloping toward base. Base setose like rest of body whorl, with zone of smaller setae around umbilical region. Last whorl not markedly descending; last 0.2 turn sometimes rising slightly on penultimate whorl; body whorl sharply constricted behind lip. Aperture broadly auriculate, peristome concave in profile, oblique, at angle of about 45° to vertical; lip strongly expanded, reflected at base, thickened submarginally. Umbilical crevice extremely narrow, oblique. Basal lip straight to gently arched; inner part narrowed, often with a small callus nodule. Inner lip excavated, deeply entering at columella, dilated so that it encroaches on, and nearly covers, umbilicus from front. Parietal callus smooth, shining, with fine granulation, free edge convex, swinging to left of umbilicus, with small sinus below upper limb of peristome. Prominent, short, elevated, white parietal lamella present. Shell light golden brown; peristome light orange to pinkish

Dimensions of holotype: Diameter (exclusive of expanded lip) 16.2 mm, height 8.9 mm, whorls 5.9.

Measurements and counts of material at hand: Range of adult shell diameter 12.5-16.2 mm (mean of 36 specimens



Figures 22-24

Vespericola klamathicus Roth & Miller, sp. nov. Holotype, shell, SBMNH 142588, CALIFORNIA: Humboldt County: Aiken Creek, NE of Weitchpec, for 0.3 km upstream (west) of California Highway 96. W. B. Miller, B. Roth coll., 8 April 1992; top, side, and basal views. Diameter 16.0 mm.

including holotype, 14.57 mm); height, 7.5–9.5 mm ($\bar{\mathbf{x}}$ = 8.73 mm); height/diameter ratio, 0.55–0.64 ($\bar{\mathbf{x}}$ = 0.600); number of whorls, 5.5–6.2 ($\bar{\mathbf{x}}$ = 5.89).

Description of soft anatomy: Three topotypes and five specimens from a nearby locality (Wilson Creek) were dissected.

Living animal light tan to pinkish buff along foot, darker and grayer on body-stalk. Mantle over the lung clear buff, 25-40% maculated with black.

Atrium (Figure 20) of moderate length for the genus. Penis long, slender, cylindrical, with about 70% of its length enclosed in thin sheath adnate to base. Penial retractor muscle inserted on epiphallus. Narrow retentor muscle extending from penial retractor muscle at attachment on epiphallus to summit of penial sheath, from which other thin retentor fibers form connections with parts of epiphallus and vas deferens. Sheathed part of penis in figured topotype about 6.0 mm long; protruding part about 2.8 mm long. In other specimens, sheathed part 4.5-5.8 mm (mean 4.9 mm); protruding part 0-3.4 mm (mean 1.1 mm). Ratio of protruding length to sheathed length averaging about 0.3. Slender peduncular section of about 1.5 mm present between base of sheath and junction with atrium. Apex of penis containing very long, slender, acicular verge 10.0 mm long and 0.9 mm wide at its base, which extends below sheathed part of penis and recurves into peduncular section. Seminal duct opening in minute terminal cleft of verge. Inner wall of penis with oblique papillose pilasters, some of which fuse at their lower ends (Figure 20).

Spermathecal duct long, slender, cylindrical, appressed to free oviduct (which is smaller in diameter and branches from it), about 9.3 mm long, about 1.0 mm in diameter at its junction with the oviduct, tapering gradually to 0.4 mm constriction at base of spermatheca. Spermatheca oblong-ovate in fully mature specimens, narrowly cylindrical

in less mature individuals, about 4.4 mm long, with rounded tip.

Type material: Holotype: CAS 064088 (shell), CALI-FORNIA: Humboldt County: Sawmill Gulch, on Ishi Pishi Road, 2.0 mi [3.2 km] east [NE] of Orleans Ranger Station. R. R. Talmadge coll., July 1961.

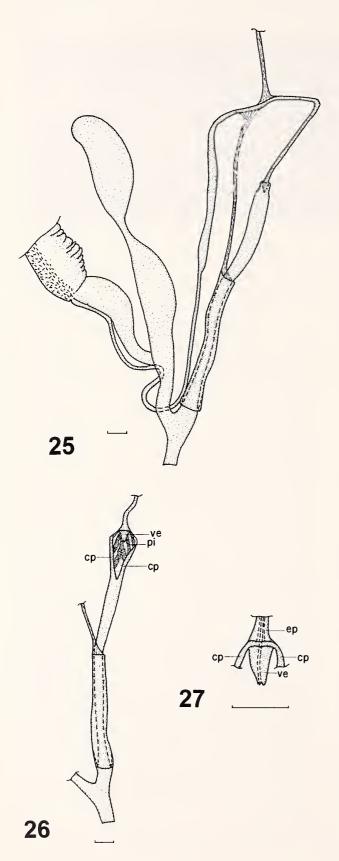
Paratypes: BR 1166, CAS 064089 (shells), from same locality as holotype. Additional paratypes stated to be deposited in ANSP, FMNH, LACM, MCZ, SDNHM, USNM, and various private collections (Talmadge, 1962).

Referred material: CALIFORNIA: Humboldt County: Wilson Creek, ca. 2.5 mi [4.0 km] NE of Orleans, upstream (west) of Ishi Pishi Road (BR 1762, SBMNH 78124); Sawmill Gulch, east and west of Ishi Pishi Road (BR 107, BR 1167, BR 1438, BR 1758, SBMNH 78119); N side of Sawmill Gulch (CAS 053475).

Remarks: Vespericola karokorum is distinguished anatomically from other species by its extremely long verge and long spermathecal duct. In no other known species of Vespericola does the verge come close to equalling the length of the penis. In concluding that V. karokorum was a "microgeographic race" of V. megasoma, Hunt & DeMartini (1979) evidently did not examine the verges. Vespericola karokorum also differs from the other species described herein in that the penial sheath covers well over half of the penis (occasionally reaching the apex of the penis), and the spermathecal duct is slender and cylindrical, not swollen and ovate.

Hunt & DeMartini (1979) reported *V. karokorum* from 15 localities ranging from Reynolds Creek (sec. 18, T. 12 N, R. 6 E, Humboldt Base and Meridian) to Whitmore Creek (sec. 21, T. 11 N, R. 6 E). We have not reviewed their material.

The species is found in leaf litter and under stones, branches, and debris on the ground along streams.



Vespericola klamathicus Roth & Miller, sp. nov. (Figures 22-27)

Diagnosis: A medium-sized to large *Vespericola* with depressed-globose, almost imperforate shell of 5.75–6.5 whorls; whorls flattened, with deeply impressed to channeled suture; periostracal setae 11–27/mm². Penis long, slender, cylindrical, containing short, conical verge with cleft tip; penial sheath covering somewhat more than half of penis.

Description of shell: Shell medium-sized for the genus, depressed-globose, almost imperforate, of 5.75–6.5 whorls; base inflated, solid-looking. Spire low-domed to broadly conic, its sides weakly convex; whorls flattened; suture strongly impressed to channeled. Embryonic whorls 1.4-1.7, sculptured with low riblets radiating from suture, more or less completely broken into rows of blunt papillae. Early neanic whorls with fine, crowded, slightly retractive growth rugae and rather sparse, erect or gently curving, acicular setae in protractive, descending rows (also aligning in nearly collabral series). Periostracum between setae radially wrinkled and irregularly granulose; granules becoming obsolete on body whorl. Setae shorter, more regularly spaced, and usually closer together on subsequent whorls; 11-27 setae/mm² on body whorl. Periphery inflated, broadest above middle of whorl, somewhat sloping toward base. Base densely and regularly setose; setae smaller than on shoulder of whorl. Last whorl not markedly descending, compressed upward and sharply constricted behind lip. Aperture broadly auriculate, peristome concave in profile, oblique, at angle of about 35° to vertical; lip expanded and reflected, most strongly at base, moderately thickened submarginally. Umbilical crevice extremely narrow, oblique. Basal lip straight; inner part narrowed, slightly kinked forward, usually with low callus nodule. Inner lip dilated, nearly covering umbilicus from front. Parietal callus granulose, free edge strongly convex, swinging well to left of umbilicus, with small, rather acute sinus below upper limb of peristome. Prominent, white, triangular, convex-forward parietal lamella present. Shell light reddish brown; peristome white to pinkish tan.

Figures 25–27

Vespericola klamathicus Roth & Miller, sp. nov. Drawings made from projections of stained whole mounts. Scale line = 1 mm. Figure 25. Anterior part of reproductive system of holotype, SBMNH 142588, CALIFORNIA: Humboldt County: Aiken Creek, NE of Weitchpec, for 0.3 km upstream (west) of California Highway 96. W. B. Miller, B. Roth coll., 8 April 1992. Figure 26. Penial complex of paratype, SBMNH 142589, with penis cut open to show verge and pilasters; same locality as above. Figure 27. Verge of paratype, SBMNH 142589, magnified to show cleft apex and seminal duct; same locality as above.

Dimensions of holotype: Diameter (exclusive of expanded lip) 16.0 mm, height 10.6 mm, whorls 6.25.

Measurements and counts of material at hand: Range of adult shell diameter 13.4–16.4 mm (mean of 31 specimens including holotype, 15.15 mm); height, 9.0–10.8 mm ($\bar{\mathbf{x}} = 10.11$ mm); height/diameter ratio, 0.61–0.70 ($\bar{\mathbf{x}} = 0.668$); number of whorls, 5.75–6.5 ($\bar{\mathbf{x}} = 6.11$).

Description of soft anatomy: The holotype and five paratypes were dissected; an additional 10 specimens from nearby localities (Crawford Creek and Red Cap Gulch) also were dissected.

Living animal light tan, darker and grayer on bodystalk. Mantle over the lung clear buff, 10-30% maculated with black.

Atrium (Figure 25) of moderate length for the genus. Penis long, slender, and cylindrical, with anterior, basal half or more enclosed in thin sheath adnate to base. Penial retractor muscle inserted on the epiphallus. Narrow retentor muscle extending from penial retractor muscle at attachment on epiphallus to summit of penial sheath, from which other thin retentor fibers form connections with parts of epiphallus and vas deferens. Sheathed part of penis in holotype about 7.2 mm long; protruding part about 5.9 mm long. In paratypes, sheathed part 4.4-6.5 mm (mean 5.6 mm); protruding part 6.0-8.8 mm (mean 7.2 mm). Ratio of protruding length to sheathed length 1.0-1.7 (mean 1.32). Broad peduncular section of about 0.8 mm present between base of sheath and junction with atrium. Apex of penis containing short, conical, pointed verge 0.6 mm long and 0.4 mm wide at its base. Seminal duct opening into penial chamber at tip of verge through minute cleft about 0.1 mm long (Figure 27). Inner wall of penis with papillose, oblique pilasters.

Spermathecal duct massive, long, appressed to free oviduct (which is smaller in diameter and branches from it), elongate-ovate, about 7.0 mm long, about 1.0 mm in diameter at its junction with the oviduct, tapering gradually to 0.3 mm constriction at base of spermatheca. Spermatheca oblong-ovate in fully mature specimens, narrowly cylindrical in less mature individuals, about 6.0 mm long, with blunt tip.

Type material: *Holotype:* SBMNH 142588 (shell and stained whole mount of reproductive system), CALIFORNIA: Humboldt County: Aiken Creek, NE of Weitchpec, for 0.3 km upstream (west) of California Highway 96. W. B. Miller, B. Roth coll., 8 April 1992.

Paratypes: SBMNH 142589 (5 shells and stained whole mounts of reproductive system), BR 1759 (2 shells), from same locality as holotype. Additional paratypes (all, CALIFORNIA: Humboldt County:) SBMNH 78121, BR 1760, Crawford Creek, for 0.2 km upstream (north) of California Highway 96. W. B. Miller, B. Roth coll., 9 April 1992. SBMNH 78122, BR 1761, Red Cap Gulch, for 0.2 km upstream (north) of California Highway 96. W. B. Miller, B. Roth coll., 9 April 1992. Additional paratypes deposited in ANSP, CAS, LACM, and USNM.

Referred material: CALIFORNIA: Humboldt County: Pecwan (SBMNH, BR 1097); Camp Creek (BR 1863); mouth of Ullathorne Creek (CAS 052422); Ullathorne Creek (CAS 052272); Slate Creek (SBMNH); Weitchpec (SBMNH); 8.8 km S of Weitchpec (BR 956); Pull Creek (BR 1168); Mill Creek, Hoopa Valley Reservation (SBMNH).

Remarks: Vespericola klamathicus is distinguished anatomically from other species by its very long, slender, cylindrical penis containing a short, conical verge with a cleft tip. The genitalia most resemble those of V. eritrichius, but in V. eritrichius the tip of the verge is not cleft, the vagina is longer, and a fleshy thickening is present just below the junction of oviduct and spermathecal duct.

The high average whorl count (6.11) and flattened whorl profile with deeply impressed to channeled suture are distinctive characters of the shell of V. klamathicus. At the type locality, setae range from 11 to $26/\text{mm}^2$. In all material examined, setae range from 11 to $27/\text{mm}^2$ (mean 19.9).

Hunt & DeMartini (1979) reported "Vespericola megasoma" from 24 localities ranging from Blue Creek (sec. 26, T. 14 N, R. 4 E, Humboldt Base and Meridian) to the North Fork of Mill Creek (sec. 21, T. 9 N, R. 6 E). We have not reviewed this material, but much or all of it may be V. klamathicus.

The species is found among leaf litter and under debris on the ground along streams.

Etymology: The species is named for the Klamath Mountains. For purposes of the American Fisheries Society list of the common names of mollusks (Turgeon et al., 1988) and other administrative uses, we propose the name "Klamath hesperian."

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